CHROMOSOME COUNTS IN THE SECTION SIMIOLUS OF THE GENUS MIMULUS (SCROPHULARIACEAE). V. THE CHROMOSOMAL HOMOLOGIES OF M. GUTTATUS AND ITS ALLIED SPECIES AND VARIETIES

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The purpose of this study[1] was to investigate the chromosomal homologies of *Mimulus guttatus* and its allied species and varieties. This was done by observing the pairing behavior of the chromosomes in the pollen mother cells of F_1 and a few F_2 hybrid plants obtained from crossing various members of the *M. guttatus* complex and its related taxa. This large, highly polymorphic group (Grant, 1924; Pennell, 1951) of gay-looking, yellow-flowered plants consists of a vast number of typically isolated populations of various sizes, of differing combinations of morphological characteristics, and of assorted taxonomic ranks. Its populations grow by springs and streams from the Aleutian Islands to southern Mexico and from the Pacific coast to the Mississippi River in North America, and in the Andes and their foothills in South America.

Of these populations, thirty-seven which exhibited much of the morphological variation and much of the diversity of geographical origin of the entire group were sampled for this investigation. The thirty-seven cultures which were grown from these populations represented at least eighteen different species and varieties (table 1). They included all of the most common forms of the group as well as several rare ones. These representative cultures were crossed in all possible combinations (Vickery, 1956a, 1956b) and most of the resulting seeds were sown. Some of the combinations failed to produce flowering hybrids due to the presence of crossing barriers of various strengths (Vickery, 1956a, 1956b, 1959). Consequently the cytological analysis was limited to the successful hybrids (table 2), which were chiefly combinations of *M. guttatus* with each of the related species plus a few combinations among the latter.

The method of fixing the buds was the same as that employed in the previous investigations (Mukherjee and Vickery, 1959, 1960); i.e., fixation in 2 parts absolute ethanol to 1 part glacial acetic acid saturated with ferric acetate. After 24 hours in the fixative, the buds were transferred to 70% ethanol if they were to be stored for later study. In preparing the slides, the anthers were dissected from the buds and then squashed in a drop of iron-aceto-carmine stain. In many cases the most interesting hybrids produced only one to several flowers which in turn might or might not yield one or more cells suitable for cytological examination. Conse-

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quently many of our counts are based on suboptimum numbers of cells. Nevertheless certain trends are clearly apparent in the results. Most of the cells analyzed were drawn with the aid of a camera lucida and many were photographed. In addition, numerous F_1 hybrid plants were pressed, mounted, and deposited for future reference in the Garrett Herbarium of the University of Utah.

The chromosomes of the different species and varieties ranged in size from dots as small as one-half micron in diameter to ovals as large as one micron wide by two micra long (see figure 1 and the previous papers of this series). Despite this variation in size, which probably was due in part to differing orientations of the chromosomes in the cells, the chromosomes were so similar in general appearance that rarely could we identify the individual chromosomes contributed by each parent to a particular F_1 hybrid. Therefore, our analysis of chromosomal homologies was carried out at the genome level rather than at that of the individual chromosomes. We observed the amount and regularity of chromosome pairing in as many pollen mother cells as possible in over 60 different interspecific and intervarietal hybrids (table 2).

In our cytological examinations of the parental species and varieties (Vickery, 1955; Mukherjee, Wiens, and Vickery, 1957; Mukherjee and Vickery, 1959, 1960), we found no indication of true autosyndesis in any of the cultures. However, under the fixation schedule employed, several of the annual races of *M. guttatus* exhibited chromosome stickiness which simulated autosyndesis and secondary chromosome associations (Vickery, 1959). This difficulty was overcome by techniques suggested by Doctors Harlan Lewis and Henry J. Thompson of the University of California at Los Angeles.

According to our findings, the basic genome in the group appears to be that of the diploid species, specifically, of the type of *M. guttatus* with its n=14 chromosomes. Possibly *M. guttatus* and/or the other diploid species such as *M. nasutus, M. glabratus* var. *utahensis, M. tilingii,* etc. (see table 1) may be ancient tetraploids inasmuch as a distantly related species, *M. mohavensis* Lemmon, has n=7 chromosomes (Carlquist, 1953). However, at the present time there is no evidence for this hypothesis. Therefore, tentatively we may consider the whole group, *M. guttatus* and its relatives, to consist of species and varieties at the diploid (n=13, 14, 15), tetraploid (n=26, 30, 31, 32), and hexaploid (n=45, 46) chromosomal levels, with one to several examples of aneuploidy at each level. The data at hand suggest to us that this polyploid series is built up on a base number of x=15 which presumably is an aneuploid derivative of the basic genome of n=14 chromosomes so commonly found in this group of species.

Despite the tremendous range of morphological and physiological variation within *M. guttatus* itself (Grant, 1924), all of its populations thus far counted have n=14 chromosomes. The chromosomes of the interpopulation F_1 hybrids exhibited normal chromosome pairing (table 2)

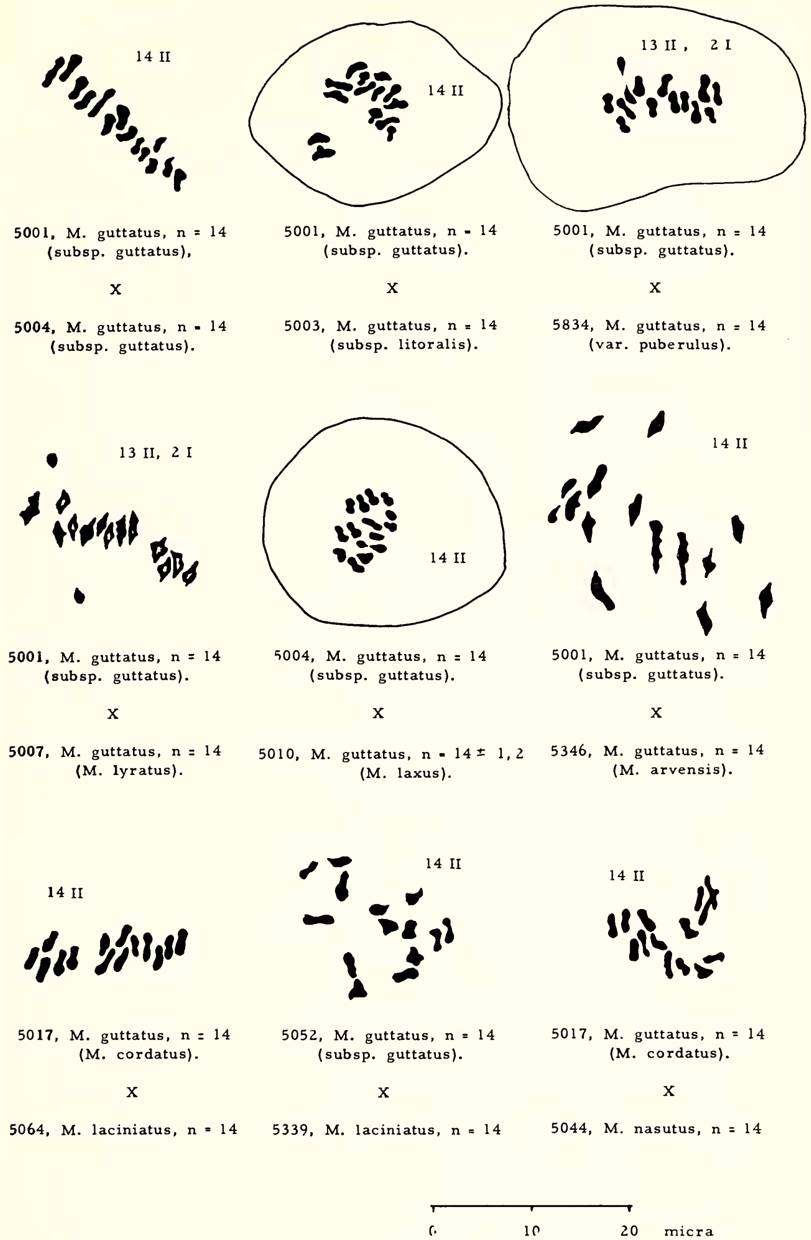


FIG. 1. Meiotic chromosomes of intraspecific F_1 hybrids of the *Mimulus guttatus* complex as defined in this article. All configurations at or near first metaphase. Camera lucida drawings at an original magnification of $\times$ 2,520, reduced to $\times$ 1,260.

except in a few cases which were probably the result of factors of technique. One exception turned up in the lone intra-*guttatus* F_2 hybrid plant analyzed (5346 × 5839), which had an extra chromosome.

Due in part to this generally pervasive cytological homogeneity, *M. guttatus* has been treated in this article in the broad sense of Grant (1924). Except for *M. platycalyx*, the various species segregated from *M. guttatus* by Pennell (1951) have been included in it (table 1). Several of our cultures could be assigned to these segregate species, specifically, culture 5007 to *M. lyratus*, 5017 to *M. cordatus* [so identified by F. W. Pennell (see *Alexander & Kellogg 2844*, UC 696,020, from which our seeds came)], 5010 to *M. laxus*, and 5346 to *M. arvensis* (table 1.) However, these species intergrade morphologically with each other and with *M. guttatus*. Cytologically, they all appear to possess the same genome (figure 1). Genetically, they are fully interfertile or else separated by no stronger barriers than those that occur within *M. guttatus* in the strict sense (Vickery, 1959). Therefore, with these facts in mind, we have treated *M. lyratus, M. cordatus, M. laxus*, and *M. arvensis* as synonyms of *M. guttatus*.

Two of the *M. guttatus* cultures, 5009 and 5010, from Mather, California, were known to be aberrant in that they occasionally produced microspores with n=13, 15, or 16 chromosomes instead of the usual n=14 (Mukherjee and Vickery, 1959). The present investigation showed that at least some of these aneuploid microspores were functional as can be observed in the chromosome complements of their F_1 hybrids (figure 2 and table 2). A comparable situation was observed in *M. luteus* (table 2) and in *M. glabratus* var. *fremontii* (figure 4). These facts are significant because they indicate a likely mechanism for the production of aneuploid plants. Possibly the already-mentioned intra-*guttatus* F_2 plant (5346 × 5839) with the extra chromosome arose in this manner. Such aneuploid plants might in turn lead to the establishment of aneuploid populations and even, eventually, of aneuploid varieties and species such as commonly occur in the *M. guttatus* complex and its relatives (table 1).

Mimulus guttatus hybridized readily with *M. laciniatus*, with the n=14 form of *M. nasutus*, and with *M. glaucescens*. In the first two cases the hybrids were fertile and their pollen mother cells exhibited regular chromosome pairing, although the regularity of chromosome pairing was considerably decreased in the F_2 individuals studied. The F_1 hybrids of *M. guttatus* × *M. glaucescens* were nearly sterile, and their chromosomes showed reduced pairing (figure 2 and table 2). Probably *M. laciniatus* and *M. nasutus* should be considered simply as well-marked varieties of *M. guttatus*, whereas *M. glaucescens* should be treated as a nearly distinct species.

Mimulus platycalyx (n=15) and the n=13 form of *M. nasutus* both hybridized with *M. guttatus*, but the F_1 hybrids produced were partially sterile (Vickery, 1956b). The chromosomes in the pollen mother cells of the hybrids showed regular pairing of 13II and 1I for *M. guttatus*

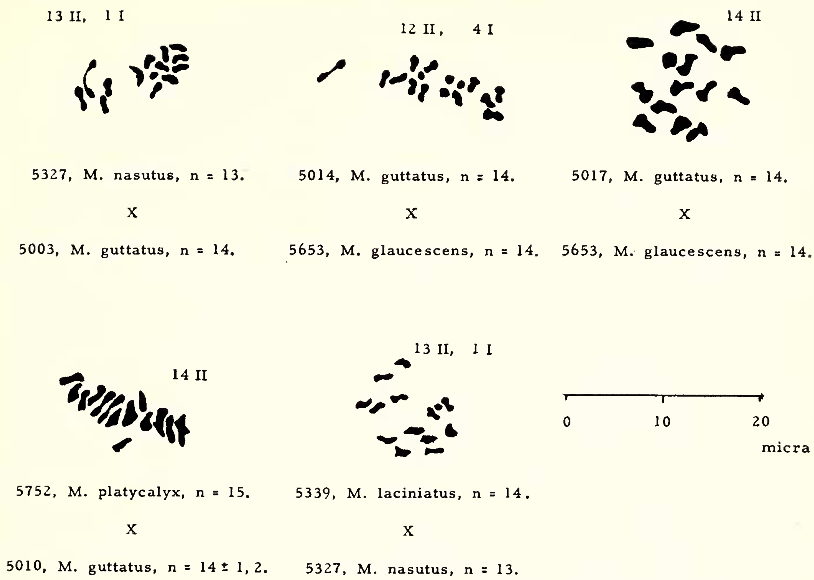


FIG. 2. Meiotic chromosomes of interspecific F_1 hybrids of *Mimulus guttatus* complex. All configurations at or near first metaphase. Camera lucida drawings at an original magnification of × 2,520, reduced to × 1,260.

× *M. nasutus* and 14II and 1I for *M. guttatus* × *platycalyx* except where the aberrant culture 5010 was a parent (figure 2 and table 2). Despite the aneuploidy and genetic differentiation of these species, both their genomes appear to be basically homologous to that of *M. guttatus*, just as the genomes of the various aneuploid species of section *Alatae* of *Nicotiana* are homologous (Goodspeed, 1954). Clearly, both species are an integral part of the *M. guttatus* complex although their accurate specific designation must await a detailed study of the relevant literature and type specimens.

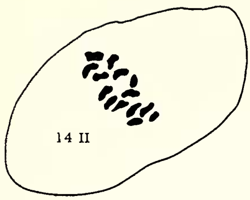
One of the F_1 hybrids of *M. nasutus* (5751; n = 14), × *M. nasutus* (5327; n = 13), which would be expected from the foregoing results to show marked sterility was highly fertile instead (Vickery, 1956b). It set an average of 50 seeds per capsule whereas the hybrid resulting from the reciprocal combination averaged only 3 seeds per capsule. The cytological analysis of several pollen mother cells of one of the F_2 hybrids of the highly fertile cross provided the explanation. The fertile hybrid was an amphiploid with n = 27 chromosomes (table 2).

The alpine species *M. tilingii* did not hybridize readily with *M. guttatus*. The hybrids that were formed with the exception of two possible amphiploids, produced sterile flowers if they flowered at all. However, the pollen mother cells of these F_1 hybrids of *M. guttatus* × *M. tilingii* exhibited regular chromosome pairing in three of the four cells available for study (figure 3 and table 2). These cells came from hybrids involving both the n=14 and n=15 races of *M. tilingii* var. *tilingii*. Therefore, the basic, or what we may call the *M. guttatus* genome of chromosomes, probably is present in both the chromosomal races of *M. tilingii* var. *tilingii* also, although the crossing barriers between this species and the *M. guttatus* complex are so nearly complete as to warrant its exclusion from the complex. In fact, *M. tilingii* is itself the main species of another complex of related species and varieties.

Mimulus tilingii var. *corallinus* (n=24) forms completely sterile hybrids with *M. guttatus* and with *M. tilingii* var. *tilingii*. In the majority of the pollen mother cells examined in the F_1 hybrids of *M. guttatus* × *M. tilingii* var. *corallinus*, the chromosomes showed 14II and 10I (figure 3 and table 2). In a few cases trivalent chromosome associations were observed which suggest the presence of at least a few residual homologies between some of the additional ten chromosomes of *M. tilingii* var. *corallinus* and the basic genome. The extra ten chromosomes constitute a second genome which appears to be incomplete on the basis of the other known chromosome numbers in the group (table 1). Possibly it is a highly modified derivative of the basic genome. However, its origin and relationships have yet to be determined precisely. *Mimulus tilingii* var. *corallinus* warrants specific rank, but its accurate designation must also, as with the members of the *M. guttatus* complex, await an opportunity to study the literature and type specimens involved.

Mimulus guttatus will hybridize with South American *M. luteus* (n=30, 31, or 32), but the hybrids are completely sterile. The chromosomes in the pollen mother cells of the hybrids show considerable pairing (figure 3 and table 2). In some cases the number of pairs exceeds that of the basic genome, which must mean that *M. luteus* chromosomes are, at least occasionally, pairing with each other. However, inasmuch as there was no indication of autosyndesis in *M. luteus* itself (Mukherjee and Vickery, 1960), probably most of the paired chromosomes are homologues coming from *M. guttatus* or *M. tilingii* on the one hand and from *M. luteus* on the other. Therefore the basic genome appears to be present in *M. luteus* though in slightly modified form. The second genome of *M. luteus* may be a drastically modified form of the basic genome, but its true origin and relationship is not clearly demonstrated by the available data.

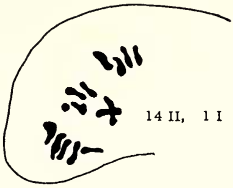
Mimulus guttatus formed nearly sterile hybrids with *M. glabratus* var. *utahensis* (n=14). Typically the chromosomes of the pollen mother cells of these hybrids exhibited 13 bivalent and 2 univalent chromosome configurations at the first metaphase stage of meiosis (figure 4 and table 2). Apparently the two genomes are essentially homologous, but one pair of chromosomes has become so modified as to synapse only rarely. Therefore, in view of the sterility of the F_1 hybrids and the slight cytological differentiation of these species and despite the morphological similarity, *M. glabratus* var. *utahensis* should not be included in the *M. guttatus* complex of species. It is an integral part of the large, widespread, and varied *M. glabratus* complex.



5017, M. guttatus, n = 14.

x

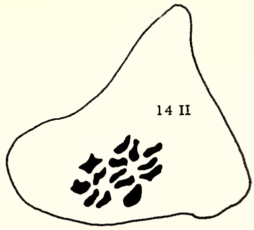
5012, M. tilingii var. tilingii, n = 14.



5967, M. tilingii var. tilingii, n = 15.

x

5052, M. guttatus, n = 14.



5689, M. tilingii var. tilingii, n = 14.

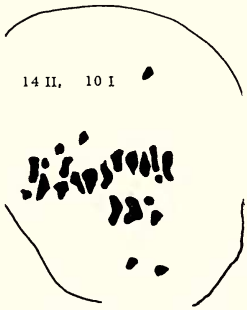
x

5012, M. tilingii var. tilingii, n = 14.

5011, M. tilingii var. corallinus, n = 24.

x

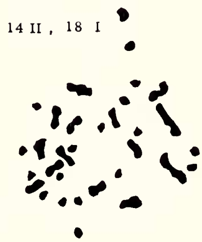
5052, M. guttatus, n = 14.



5011, M. tilingii var. corallinus, n = 24.

x

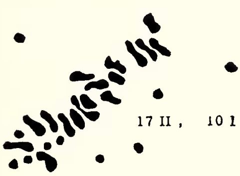
5007, M. guttatus, n = 14.



5052, M. guttatus, n = 14.

x

5043, M. luteus, n = 32.



5012, M. tilingii, n = 14.

x

5043, M. luteus, n = 32.

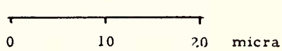


FIG. 3. Meiotic chromosomes of interspecific F_1 hybrids of *Mimulus guttatus* complex with *M. tilingii* and *M. luteus* complexes, etc. All configurations at or near first metaphase. Camera lucida drawings at an original magnification of $\times$ 2,520, reduced to $\times$ 1,260.

The pollen mother cells of the F_1 hybrids of *M. tilingii* var. *tilingii* $\times$ *M. glabratus* var. *utahensis* (5012 $\times$ 5747) frequently exhibited a small extra chromosome and hence were n=15. The extra chromosome was probably a B chromosome from culture 5747, because it was not observed in culture 5012 (culture 5747 has yet to be studied cytologically). Furthermore, both parental forms are known to contain other populations with n=15 chromosomes (Mukherjee, Wiens, and Vickery, 1957; Mukherjee and Vickery, 1959).

As with the preceding variety, *M. guttatus* formed nearly completely sterile F_1 hybrids with *M. glabratus* var. *fremontii* (n=30, 31). However, the pollen mother cells of these hybrids displayed much variation in the pairing behavior of their chromosomes (table 2). They showed the least amount of consistent pairing of any of the hybrids studied. They averaged

TABLE 1. ORIGIN OF CULTURES USED IN THE CYTOGENETIC INVESTIGATION OF THE RELATIONSHIP OF MIMULUS GUTTATUS AND ITS SPECIES

Species, culture, and chromosome number	**Origin and Collector**
M. guttatus DC.	
(*M. guttatus* DC. subsp. *guttatus*)	
5001, n=14	Pacific Grove, Monterey County, California, altitude 5 feet, *Vickery 1* (UT).
5004, n=14	Chew's Ridge, Monterey County, California, altitude 4,500 feet, *Vickery 3* (UT).
5015, n=14	Mono Inn, Mono County, California, altitude 6,450 feet, *Clausen 2043* (UT).
5052, n=14	Mt. Diablo, Contra Costa County, California, altitude 1,000 feet, *Stebbins 703* (UT).
(*M. guttatus* subsp. *litoralis* Pennell)	
5003, n=14	Pescadero, San Mateo County, California, altitude 30 feet, *Clausen 2083* (UT).
(*M. guttatus* var. *puberulus* [Greene] Grant)	
5006, n=14	Yosemite Junction (rocky creek), Tuolumne County, California, altitude 1,300 feet, *Hiesey 560* (UT).
5009, n=14 ± 1 or 2	Mather (Hog Ranch meadow), Tuolumne County, California, altitude 4,600 feet, *Hiesey 571* (UT).
5014, n=14	Lee Vining Canyon, Mono County, California, altitude 8,000 feet, *Clausen 2039* (UT).
5753, n=14	Stanislaus River, Tuolumne County, California, altitude and collector uncertain.
5834, n=14	Salt Lake City, Salt Lake County, Utah, altitude 4,400 feet, *Vickery 330* (UT).
5835, n=14	Centerville, Davis County, Utah, altitude 4,360 feet, *Vickery 331* (UT).
5837, n=14	Fish Haven, Bear Lake County, Idaho, altitude 6,100 feet, *Vickery 322* (UT).
5839, n=14	Big Cottonwood Canyon, Salt Lake County, Utah, altitude 7,100 feet, *Vickery 334* (UT).
5864, n=14	Skaggs Springs, Sonoma County, California, altitude ca. 50 feet, *R. W. Holm*, Spring 1951, unmounted.

Species, culture, and chromosome number	Origin and Collector
(*M. lyratus* Bentham)	
5007, n=14	Yosemite Junction (marsh), Tuolumne County, California, altitude 1,350 feet, *Hiesey 559* (UT).
(*M. laxus* Pennell)	
5010, n=14 ± 1 or 2	Mather (Hog Ranch spring area), Tuolumne County, California, altitude 4,800 feet, *Hiesey 569* (UT).
(*M. cordatus* Greene)	
5017, n=14	Darwin Falls, Inyo County, California, altitude 2,500 feet, *Alexander* & *Kellogg 2844* (UC).
(*M. arvensis* Greene)	
5346, n=14	Mount Oso, Stanislaus County, California, altitude 1,000 feet, *Vickery 190* (UT).
M. laciniatus Gray	
5064, n=14	The Dardanelles, Tuolumne County, California, altitude 5,775 feet, *Alexander* & *Kellogg 3746* (UC).
5339, n=14	Lake Eleanor Road, Tuolumne County, California, altitude 4,200 feet, *Vickery 179* (UT).
M. glaucescens Greene	
5653, n=14	Richardson Springs, Butte County, California, altitude 600 feet, *Pennell* & *Heller 25,667* (UT).
M. platycalyx Pennell	
5752, n=15	Crystal Lakes Reservoir, San Mateo County, California, altitude 800 feet, *G. T. Oberlander,* April 1951 (UT).
M. nasutus Greene	
5044, n=14	Hastings Reservation, Monterey County, California, altitude 1,500 feet, *Stebbins 701* (UT).
5327, n=13	West of Yosemite Junction, Tuolumne County, California, altitude 475 feet, *Vickery 168* (UT).
M. tilingii Regel var. *tilingii*	
5012, n=14	Slate Creek, Mono County, California, altitude 10,000 feet, *Clausen 2075* (UT).
5689, n=14	Dana Plateau, Mono County, California, altitude 11,300 feet, *C. W. Sharsmith,* Aug. 21, 1950.
5690, n=14	Budd Lake, Tuolumne County, California, altitude 10,250 feet, *C. W. Sharsmith,* Sept. 13, 1950.
5967, n=15	Mount Timpanogos, Utah County, Utah, altitude 7,800 feet, *Del Wiens,* Aug. 6, 1956 (UT).
M. tilingii var. *corallinus* (Greene) Grant	
5011, n=25	Porcupine Flat, Tuolumne County, California, altitude 8,000 feet, *Hiesey 576* (UT).

Species, culture, and chromosome number	Origin and Collector
M. luteus L.	
5042, n=32	Illapel, Coquimbo, Chile, altitude 6,200 feet, *U.S.D.A. Plant Introduction number 144,535* (UT).
5043, n=30 + 0, 1 or 2	Illapel, Coquimbo, Chile, altitude 2,000 feet, *U.S.D.A. Plant Introduction number 144,536* (UT).
M. glabratus var. *utahensis* Pennell	
5048, n=14	Mono Lake, Mono County, California, altitude 6,440 feet, *Stebbins 714* (UT).
5747, n=14 + 0, or 1 B chromosome*	Pilot Cone, Mineral County, Nevada, altitude 5,550 feet, *J. Figg-Hoblein,* July 4, 1950.
M. glabratus var. *fremontii* (Bentham) Grant	
5063, n=30	Black Meadow, Black Metal Wash, Whipple Mountains, San Bernardino County, California, altitude ca. 1,200 feet, ? collector (UC).
5373, n=30, (31*)	Kakernot Springs, Alpine Creek, Brewster County, Texas, *Cory 53,186* (UT).
M. glabratus var. *parviflorus* (Lindley) Grant	
5041, n=45	Illapel, Coquimbo, Chile, altitude 4,000 feet, *U.S.D.A. Plant Introduction number 144,534* (UT).
M. pilosiusculus HBK.	
5320, n=46	Botanic Garden, Copenhagen, Denmark (Wild in Argentina, Chile, and Peru). *U.S.D.A. Plant Introduction number 181,130* (UT).

* Chromosome number based on counts in F_1 hybrids involving this culture (see table 2).

about 9 pairs per cell. Probably *M. glabratus* var. *fremontii* contains the basic genome, but in definitely modified form.

Mimulus guttatus forms nearly sterile hybrids with *M. glabratus* var. *parviflorus* (n=45) and its closely allied species *M. pilosiusculus* (n=46). The chromosomes of the pollen mother cells of these F_1 hybrids exhibited essentially regular pairing of 14II, 30I and 14II and 31I, respectively. These forms contain the basic genome plus two additional genomes. One of the additional genomes is probably homologous to the second genome of *M. glabratus* var. *fremontii* as shown by three somewhat ambiguous counts (see table 2). This hybrid, *M. glabratus* var. *parviflorus* (5041) × *M. glabratus* var. *fremontii* (5373), was hard to

Explanation of Figure 4

Meiotic chromosomes of interspecific F_1 hybrids of *Mimulus guttatus* complex with the *M. glabratus* complex, etc. All configurations at or near first metaphase. Camera lucida drawings at an original magnification of × 2,520, reduced to × 1,260.

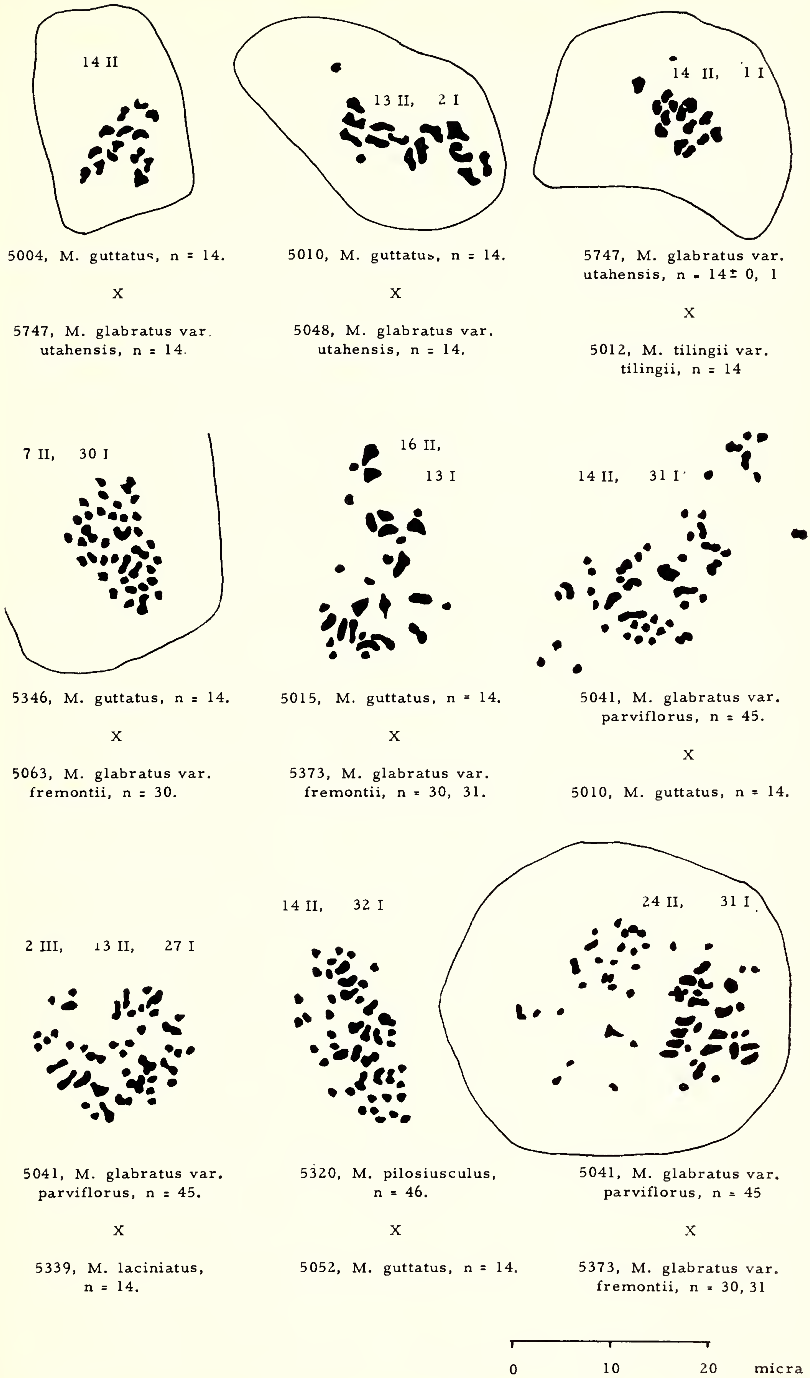


FIG. 4. Meiotic chromosomes, *Mimulus guttatus* complex and relatives, F_1 hybrids.

make and even harder to analyze cytologically. The chromosome numbers are too low for it to be a spontaneous autododecaploid instead of the true hybrid which it appeared to be on morphological grounds. We do not know how to explain the extra chromosomes, but the large number of pairs suggests to us that *M. glabratus* var. *fremontii* and *M. glabratus* var. *parviflorus* have two genomes in common. The affinities of the third genome in the South American form are not apparent from the data at hand.

The basic *M. guttatus* genome appears to be little modified in these South American forms, whereas it was slightly modified in *M. glabratus* var. *utahensis* from the Great Basin and greatly modified in *M. glabratus* var. *fremontii* from the southwestern United States. These North and South American entities of the *M. glabratus* complex probably are not as closely related as their current taxonomic status suggests (Grant, 1924; Fassett, 1939; Pennell, 1947).

In conclusion, despite the low number of pollen mother cells analyzed, the basic or *M. guttatus* genome of 14 chromosomes appears to be present

TABLE 2. PAIRING BEHAVIOR OF MEIOTIC CHROMOSOMES IN F_1 AND A FEW F_2 HYBRIDS OF MIMULUS GUTTATUS AND ITS RELATIVES.

Combinations of parental species and varieties	Culture numbers of the parents	Number of PMC's examined and pairing behavior
F_1 HYBRIDS		
guttatus × *guttatus*	5001 × 5003	1-14II
n=14 n=14	5001 × 5004	4–14II
	5001 × 5006	12–14II*
	5001 × 5007	2–14II; 1–13II, 2I
	5001 × 5009	2–14II†
	5001 × 5010	5–14II†
	5001 × 5052	1–14II
	5001 × 5346	3–14II
	5001 × 5753	4–14II
	5001 × 5834	1–14II; 1–13II, 2I 1–12II,, 4I 1–11II, 6I
	5003 × 5839	3-14II
	5004 × 5006	8–14II*
	5004 × 5010	1–14II†
	5006 × 5834	3–14II*
	5009 × 5010	1–14II†
	5014 × 5834	2–14II
	5052 × 5006	10–14II*
	5052 × 5837	1–14II
	5753 × 5001	7–14II
	5835 × 5834	3–14II
guttatus × *laciniatus*	5017 × 5064	3–14II
n=14 n=14	5017 × 5339	2–14II
	5052 × 5339	4–14II
	5064 × 5017	2–14II

Combinations of parental species and varieties	Culture numbers of the parents	Number of PMC's examined and pairing behavior
guttatus × *glaucescens*	5014 × 5653	1–12II, 4I
n=14 n=14		2–11II, 6I
	5017 × 5653	4–14II
	5837 × 5653	4–14II, 1–11II, 6I
guttatus × *platycalyx*	5017 × 5752	3–14II, 1I
n=14 n=15	5752 × 5010	1–14II; 1–13II, 2I;
		1–12II, 4I†
guttatus × *nasutus*	5017 × 5044	3–14II
n=14 n=14		
guttatus × *nasutus*	5017 × 5327	2–13II, 1I
n=14 n=13	5327 × 5003	2–13II, 1I
guttatus × *tillingii* var. *tilingii*	5012 × 5052	1–3II, 22I
n=14 n=14	5017 × 5012	1–14II
guttatus × *tilingii* var. *corallinus*	5010 × 5011	1–14II, 10I†
n=14 n=24	5011 × 5007	7–14II,10I
	5011 × 5052	1–4III, 10II, 6I;
		2–3III, 12II, 5I;
		1–14II, 10I
guttatus × *luteus*	5017 × 5043	1–1III, 11II, 19I;
n=14 n=30, 31, 32		1–10II, 25I
	5052 × 5043	1–16II, 12I;
		1–15II, 14I;
		3–14II, 18I
guttatus × *glabratus* var. *utahensis*	5004 × 5747	2–14II
n=14 n=14	5010 × 5048	11–13II, 2I†
	5017 × 5747	3–13II, 2I
	5837 × 5747	4–14II
guttatus × *glabratus* var. *fremontii*	5014 × 5373	1–44I
n=14 n=30, 31	5015 × 5373	1–16II, 13I;
		1–9II, 26I
	5346 × 5063	1–15II, 14I;
		1–7II, 30I
laciniatus × *nasutus*	5339 × 5327	3-13II, 1I
n=14 n=13		
glaucescens × *platycalyx*	5653 × 5752	6–14II, 1I
n=14 n=15		
tilingii var. *tilingii* × *guttatus*	5967 × 5052	2–14II, 1I
n=15 n=14		
tilingii var. *tilingii* × *tilingii* var.	5689 × 5012	3–14II
n=14 *tilingii*	5690 × 5012	1–14II
n=14		
luteus × *tilingii* var. *tilingii*	5043 × 5012	1–17II, 10I;
n=30, 31, 32 n=14		2–15II, 14I;
		1–14II, 16I
luteus × *tilingii* var. *tilingii*	5042 × 5690	2–14II, 18I
n=32 n=14		

Combinations of parental species and varieties	Culture numbers of the parents	Number of PMC's examined and pairing behavior
glabratus var. *utahensis* × *tilingii* var. *tilingii* n=14 + 0, 1 n=14	5747 × 5012	7–14II, 1I; 1–14II
glabratus var. *parviflorus* × *guttatus* n=45 n=14	5041 × 5010	3–14II, 31I†
glabratus var. *parviflorus* × *laciniatus* n=45 n=14	5041 × 5339	1–2III, 13II, 27I; 1–14II, 31I
glabratus var. *parviflorus* × *glabratus* var. *fremontii* n=45 n=30, 31	5041 × 5373	1–24II, 31I; 1–30II, 23I (and one M_{II} cell containing configuration of 31 and 40+chromosomes)
pilosiusculus × *guttatus* n=46 n=14	5320 × 5052 5320 × 5864	2–14II, 32I 2–15II, 30I*
F_2 HYBRIDS		
guttatus × *guttatus* n=14 n=14	5346 × 5839	7–14II, 1I
guttatus × *laciniatus* n=14 n=14	5052 × 5339	1–14II; 2–13II, 2I; 1–12II, 4I; 1–9II, 10I
nasutus × *nasutus* n=14 n=13	5751 × 5327	1–12II,30I

* Culture 5006 and 5864 and their hybrids were subject to chromosome stickiness due to too slow fixation.

† In culture 5009 and 5010, n=14 ± 1 or 2.

in all 18 species and varieties of the *M. guttatus* complex and its relatives in section *Simiolus* studied in this investigation. In several cases, e.g., *M. nasutus, M. platycalyx, M. tilingii,* the basic genome has been changed in number by aneuploidy. In other cases, e.g., *M. glaucescens, M. luteus, M. glabratus* var. *utahensis* and particularly in *M. glabratus* var. *fremontii,* it has been modified by mutations, as indicated by a decrease in the regularity of chromosome pairing in the F_1 hybrids. The second genome of *M. glabratus* var. *fremontii* (n=30, 31) appears to be homologous to the second genome of *M. glabratus* var. *parviflorus* (n=45), but its further relationships are not known. The homologies of the additional genomes present in the various tetraploid and hexaploid species have yet to be fully determined.

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MILO S. BAKER (1868–1961)

On January 4, 1961, the career of Milo S. Baker came to an end in his 92nd year. His was a role that closes the second dynasty of California botanists, namely those botanists who were direct career descendants of the colorful pioneers, many of whom he knew personally. His career as a plant collector of the California flora opened with the close of the last century and continued well over half of the current century, for he was very active to the end.

Born in Strawberry Point in Iowa on July 19, 1868, he came to California with his parents in 1875 to settle in Oak Run, Tehama County. At the age of twelve he was taken to San Jose, where he completed high school and entered what was then San Jose Normal School. At the end of one year he was admitted by examination to the teaching profession in the public schools of Santa Clara County. In 1887 he went to Modoc County to teach in the elementary schools. To reach his school, he walked from Redding to Bieber, a distance of almost 100 miles. He collected plants in this general area, and corresponded about them with Pro-